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SEED PRODUCTION BY THE NON-NATIVE *BRASSICA TOURNEFORTII* (SAHARA MUSTARD) ALONG DESERT ROADSIDES

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ABSTRACT

Plant biomass and seed production were quantified for *Brassica tournefortii* Gouan, Brassicaceae (Sahara mustard) from 3 sites spanning the Mojave and Sonoran deserts, in the Southwestern United States. We found strong linear relationships between plant biomass and seed production, with larger plants producing more seeds per plant ($R^2 = 0.93$) and greater seed biomass per plant ($R^2 = 0.94$). Both seed count ($R^2 = 0.93$) and seed biomass ($R^2 = 0.90$) were also greater in 0.25 m^2 plots that had higher plant biomass. These results and the law of constant final yield indicate that biomass and seed production of individual Sahara mustard plants can be higher in plots with lower densities. These data suggest that control efforts that do not remove all individuals may reduce densities but inadvertently increase net seed production within treated areas.

Key Words: Brassicaceae, disturbance, exotic, invasive, Mojave Desert, Sonoran Desert, *Brassica tournefortii*.

Brassica tournefortii Gouan (Brassicaceae [Sahara mustard]) was first recognized in Coachella Valley, California in the 1920s, and has since spread into cismontane California and throughout the Mojave and Sonoran deserts of North America (Minnich and Sanders 2000). It is regarded as one of the most invasive wildland pest plants in California (CalEPPC 1999; Cal-IPC 2005), and is being considered for addition to the Arizona noxious weed list (Ed Northam personal communication) and the Nevada noxious weed list (Dawn Rafferty personal communication). Sahara mustard is also one of the primary species targeted for control by land managers participating in the Mojave Weed Management Area in California and the Clark County Cooperative Weed Management Area in southern Nevada. Other land management units actively managing this species in the Mojave Desert include Lake Mead National Recreation Area, Joshua Tree National Park, and the Las Vegas Field Office of the Bureau of Land Management. It is also an identified management concern in the Sonoran Desert at Organ Pipe Cactus National Monument, Saguaro National Park (Sue Rutman personal communication) and the Coachella Valley National Wildlife Refuge (Cameron Barrows and Todd Stefanic personal communications), and on the Colorado Plateau at Grand Canyon National Park (Mary Zylo personal communication).

Since its introduction from the semi-arid and arid deserts of North Africa, the Middle East, and the Mediterranean regions of southern Europe, Sahara mustard has spread through the southwestern deserts of North America and is most common on roadsides, abandoned fields, and sand dunes (Minnich and Sanders 2000; Malusa et al. 2003). Roadsides offer increased soil moisture compared to the surrounding landscape, as they collect surface runoff from adjacent wildland areas during rains (Johnson et al. 1975; Vasek et al. 1975; Brooks and Lair accepted). Another advantage Sahara mustard has in establishing along roads is the formation of a sticky gel coat on seeds when they become wet, which allows seeds to adhere to vehicles (Minnich and Sanders 2000) and spread along roadsides.

Sahara mustard poses several threats to native desert vegetation. First, it has an early phenology giving it a head start over many native annual plants in utilizing soil moisture and mineral nutrients. The Mojave and Sonoran Deserts receive winter rain and annual plants typically germinate in response to rainfall events in fall and winter and bloom in early spring. Sahara mustard plants can flower as early as December, set seed as early as January, and most plants are fruiting or dead by April (Minnich and Sanders 2000; M. Brooks and J. Draper personal observations). Sahara mustard can complete its life cycle well before native plants have fully developed and reproduced (J. Holt et al. unpublished data; M. Brooks personal observations). The Sonoran Desert also receives summer monsoonal rainfall which can stimulate germination of Sahara mustard (M. Brooks personal observations), although its phenological timing in relationship to native summer annuals has not been reported. Second, Sahara mustard has the potential to create a continuous fuel load in areas where fuels

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are otherwise scarce and fires are infrequent. Historically, fires in Mojave and Sonoran Desert shrublands were infrequent due to low fuel loads between shrubs, preventing fires from spreading beyond ignition points (Brooks and Pyke 2001). The addition of extra fuel (Sahara mustard) could increase fire return intervals and many native desert species are not adapted to fire and their populations generally take much longer than non-native species to reestablish following fire (Brooks and Minnich 2006).

Desert annual plants are often referred to as ephemerals because they grow in habitats with unpredictable or infrequent resources such as precipitation (Barbour et al. 1999). Sahara mustard populations survive periods of summer drought as dormant seeds. During this life-history stage individuals are susceptible to predation from granivores and mortality from disease. The more seeds that can be produced, the safer the population is from depletion due to predation or disease before the next germination event. Seeds are also the singular unit of propagule dispersal for Sahara mustard, either when they are still within siliques attached to stem fragments and blown by wind, or after they are harvested by granivores (M. Brooks personal observation). As a result, producing more seeds means the population has a greater potential for persistence and expansion.

Efforts to control invasive annual plants such as Sahara mustard should ideally be designed to reduce inputs to the seed bank. Although removing individuals from a cohort may reduce their immediate effects on other plant species, the competitive release that can follow thinnings e.g., (Brooks 2000) may benefit remaining Sahara mustard plants. Thus, control efforts that only reduce density of Sahara mustard and do not completely remove all reproductive individuals may inadvertently increase growth and reproductive output of any Sahara mustard plants that remain.

Effective management of Sahara mustard requires knowledge of seed production and seed bank dynamics. In this paper we report patterns of seed production in Sahara mustard from the Mojave and Sonoran deserts of southwestern North America. We report seed production per individual plant and per unit area, and specifically evaluate the relationships of seed count and biomass with plant density and biomass. We focus on roadside populations, because this is where most control efforts to stop the spread of this species occur.

Methods

Sites were located in three areas in the Mojave and Sonoran deserts of California and Arizona, near the area where Sahara mustard was first collected and in the paths of its spread southeast and northeast into these deserts. The two criteria in choosing sites were that Sahara mustard be present along a paved road and in the adjacent wildland area, and that there be minimal disturbance at the site with the exception of the road itself. The three sites were located in: Coachella Valley, California along Interstate Highway 10, which is near the initial point of colonization for this species in North America (Minnich and Sanders 2000); Mohawk Dunes, located off of Interstate Highway 8 east of Yuma, Arizona; and along California State Highway 95 south of Needles, CA. Soils ranged from sandy at the Mohawk Dunes site to loamy and rocky at the Coachella Valley and Needles sites.

We sampled two microhabitats to include variation in plant production at two extremes of an environmental gradient, and two habitats to represent conditions typical of roadsides. The two microhabitats were: 1) beneath canopy–under the canopy of *Larrea tridentata* (DC.) Cov. (Zygophyllaceae [Creosote Bush]) or *Ambrosia dumosa* (A. Gray) Payne (Asteraceae [White Bursage]) shrubs; and 2) interspace–the area between shrubs that receives no shade from shrubs. The two habitats were: 1) along the roadside berm; and 2) greater than 20 m from the berm. Two replicate 0.25 m^2 plots were located within each of the two microhabitats within each of the two habitats at each of three sites, resulting in a total of 24 sampling plots.

Plants were collected soon after the foliage senesced in May 2003. Sahara mustard plants rooted within the boundaries of each 0.25 m^2 plot were carefully uprooted, the taproot was clipped directly below the rosette, and the samples were stored in paper bags until processing.

Above-ground plant density and biomass, and seed density and biomass, of Sahara mustard were measured for each sample. Plant density was defined as the number of plants rooted within each plot, and was reported to the nearest whole number. Plant biomass was determined by weighing plants prior to seed removal (to count the seeds) using an analytical balance (0.001 g precision), and reported to the nearest 0.01 g. Plants were individually weighed after they were air dried in a warehouse for 3 mo (May–July). Final dry biomass values were modified by subtracting the moisture mass, calculated using the average relative humidity of the storage space during the last month of drying (32.39%). We acknowledge this is a non-standard technique for determining dry biomass values, but we did not want to subject the seeds to oven heating since the seeds were to be used in subsequent germination and physiology studies. Seed density was determined by counting the number of seeds per plant, and reported to the nearest whole number. Seed biomass per plant was measured by collectively weighing all seeds removed from

TABLE 1. DENSITY AND BIOMASS OF SAHARA MUSTARD PLANTS AND SEEDS REPORTED AS AVERAGES (RANGE) FOR INDIVIDUAL PLANTS AND 0.25 m^2 PLOTS.

	Per Plant (n = 135)	Per Plot (n = 24)
Plant Density	n.a.	6 (1–23)
Plant Biomass (g)	4.07 (0.04–61.11)	22.92 (1.59–69.20)
Seed Count	995.75 (0–16,554)	5,601 (344–16,760)
Seed Biomass (g)	1.17 (0.00–19.05)	6.57 (0.47–21.44)

a plant, and reported to the nearest 0.01 g. Seeds were counted and weighed only if they were mature and viable. Viability was determined based on seed shape and color; seeds that were round and rust colored were considered viable as opposed to seeds that were flat or crushed and black. These guidelines to identify viable seeds were substantiated by subsequent germination tests (J. Holt et al. unpublished data).

Preliminary analyses indicated that there were no significant effects of microhabitat, habitat, or their interactions on seed production (count and biomass) at the individual or plot level. Seed production did vary significantly among sites ($P>0.05$), but the interactions of site with microhabitat and habitat were not significant. We therefore pooled the data into single analyses, using linear regression to evaluate relationships between plant characteristics (density and biomass) and seed production. We log-transformed the seed count data in order to normalize its distribution.

RESULTS

A total of 135 Sahara mustard plants were collected within the 24 plots. Mean above-ground dry biomass (±1 SE) of individual Sahara mustard plants was 4.07 ± 0.81 g, but ranged widely from 0.04 to 61.11 g (Table 1). Above-ground biomass per plot (0.25 m^2) averaged 22.92 ± 3.90 g (916,800 kg ha^{-1}; 818,585 lbs $acre^{-1}$). Density of standing plants per plot averaged 6 ± 1 plants (225,200 ha^{-1}), ranging from 1 (40,000 ha^{-1}) to 23 (920,000 ha^{-1}).

Seed counts for individual Sahara mustard plants averaged 996 ± 222 seeds, ranging from 0 to 16,554 seeds (Table 1). Seed counts per plot averaged 5,601 ± 1079 seeds (224,043,200 ha^{-1}). Total seed biomass for individual plants averaged 1.17 ± 0.27 g . Seed weights per plot averaged 6.57 ± 1.36 g (262,800 kg ha^{-1}). Of 135 plants analyzed, 11 weighed more than 10 grams and produced more than 2000 seeds, 46 plants weighed between 1 and 10 grams and produced between 300 and 2000 seeds, and 78 plants weighed less than 1 gram and produced less than 300 seeds per plant (Fig. 1a).

Larger plants produced more seeds and more total seed biomass than smaller plants. Seed count (Fig. 1a; seed count = 267(plant weight) - 90, R^2 = 0.95) and seed biomass (Fig. 1b; seed biomass = 0.32(plant weight) - 0.14, R^2 = 0.94) were both strongly related with plant size across the range of plants sampled. The size of individual seeds was also consistent across the range of plant sizes analyzed, as indicated by the strong linear relationship between seed count and seed biomass per plant (seed count = 0.22(seed biomass) - 0.15, R^2 = 0.94) (data not shown).

Seed production was highest on plots with the highest standing plant biomass. Seed count (Fig. 2a; seed count = 268(plant biomass) - 530, R^2 = 0.93) and seed biomass (Fig. 2b; seed biomass = 0.33(plant biomass) - 1.00, R^2 = 0.90) were strongly related to biomass of Sahara mustard plants per 0.25 m^2 plot. These results follow from the positive linear relationships of seed count and seed biomass per plant with plant size (Fig. 1a, b).

Although not statistically significant, seed count and biomass were lower in plots with the highest Sahara mustard densities (Fig. 3a, b).

DISCUSSION

Some individual Sahara mustard plants produced > 16,000 seeds in this study. However, the largest plants in our data set were only approximately 50% the size of many of the largest individuals found in the field during years of especially high rainfall and thus the largest individuals may produce substantially more seeds (M. Brooks, personal observation). The Sahara mustard plants used in this study were collected in 2003, a year that received below-average rainfall (Table 2). 2004 and 2005 were years of higher-than-average rainfall and Sahara mustard plants in these years were noticeably larger than in 2003.

Other weedy plants occurring in the Mojave Desert have been reported to produce widely variable numbers of seeds. Two plants in the Brassicaceae family, *Brassica nigra* (L.) Koch and *Sisymbrium altissimum* L., reportedly produce 13,400 and 80,400 seeds per plant, respectively (Stevens 1932). Russian thistle or tumbleweed (*Salsola tragus* L.) can produce 24,700 seeds per plant (Stevens 1932). A non-native annual grass common in the Mojave Desert, *Bromus madritensis* L. subsp. *rubens* (L.) Husnot, reportedly produces 446 to 575 seeds per plant (Huxman et al. 1999). *Chenopodium album* L., a weedy annual forb has been recorded as producing anywhere from 31,000 (Salisbury 1978) to 72,450 (Stevens 1932) seeds per plant

We know from the law of constant final yield (Kira et al. 1953; Hozumi et al. 1956) that as plant densities increase, plant size and seed production per plant decrease in response to

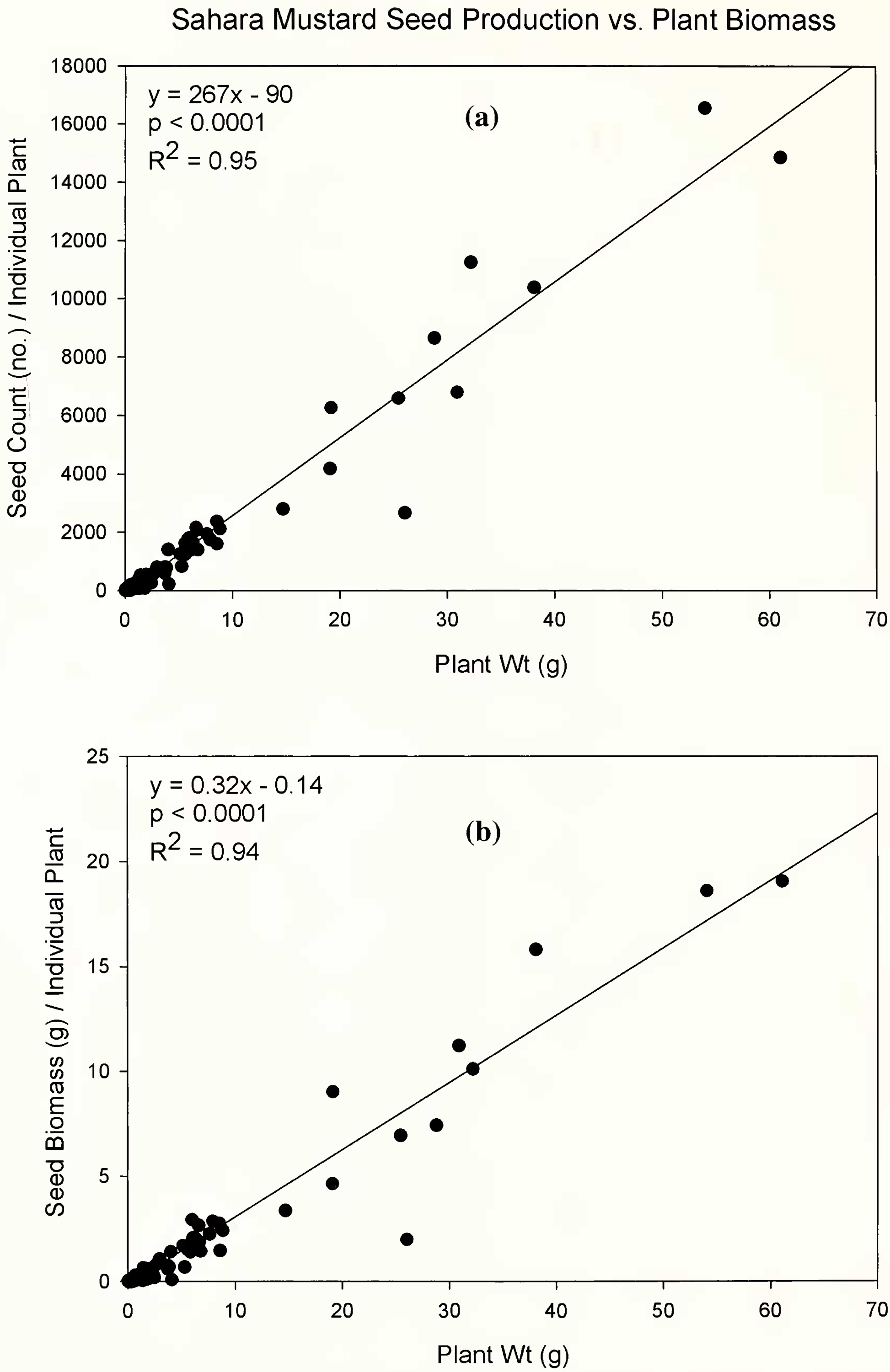
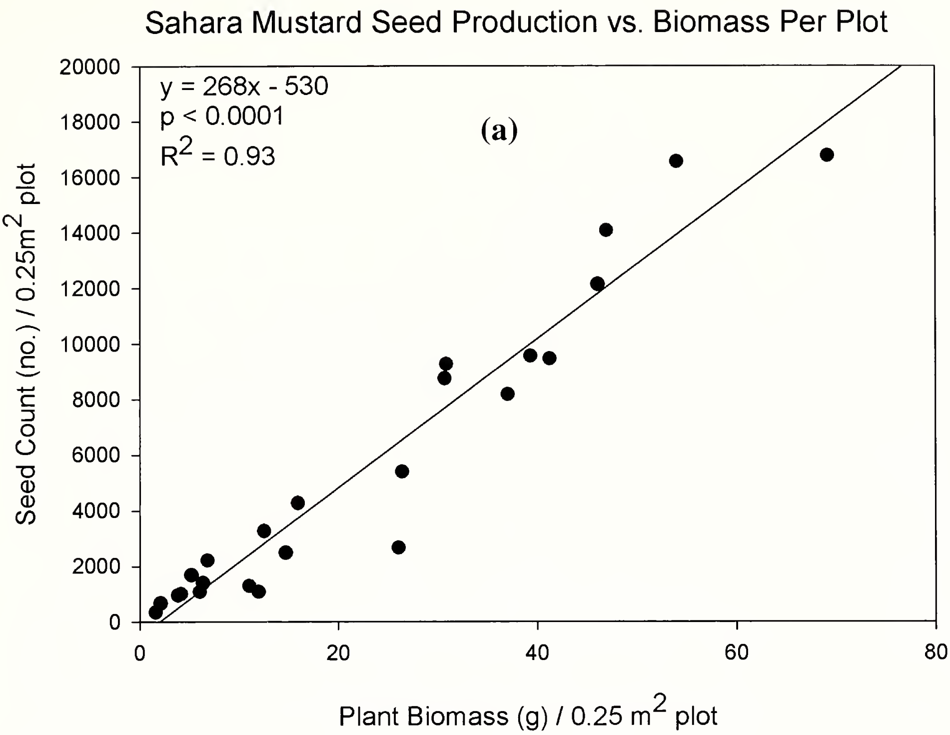


FIG. 1. **(a)** Linear correlation of seed count related to biomass per individual plant. **(b)** Linear correlation of seed biomass related to biomass per individual plant.



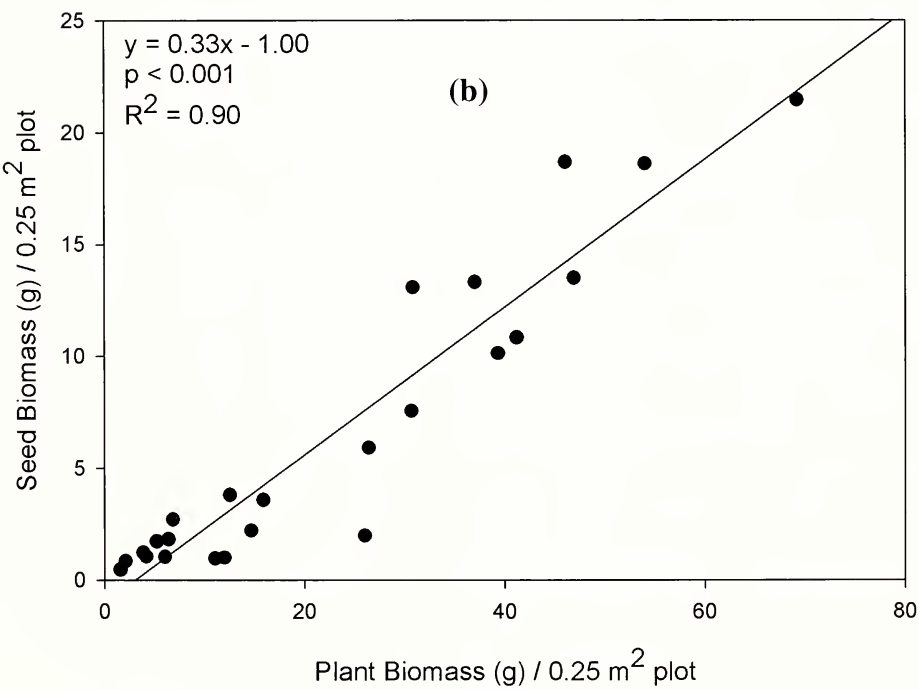


FIG. 2. **(a)** Linear correlation of seed count related to plant biomass per 0.25 m^2 plot. **(b)** Linear correlation of seed biomass related to plant biomass per 0.25 m^2 plot.

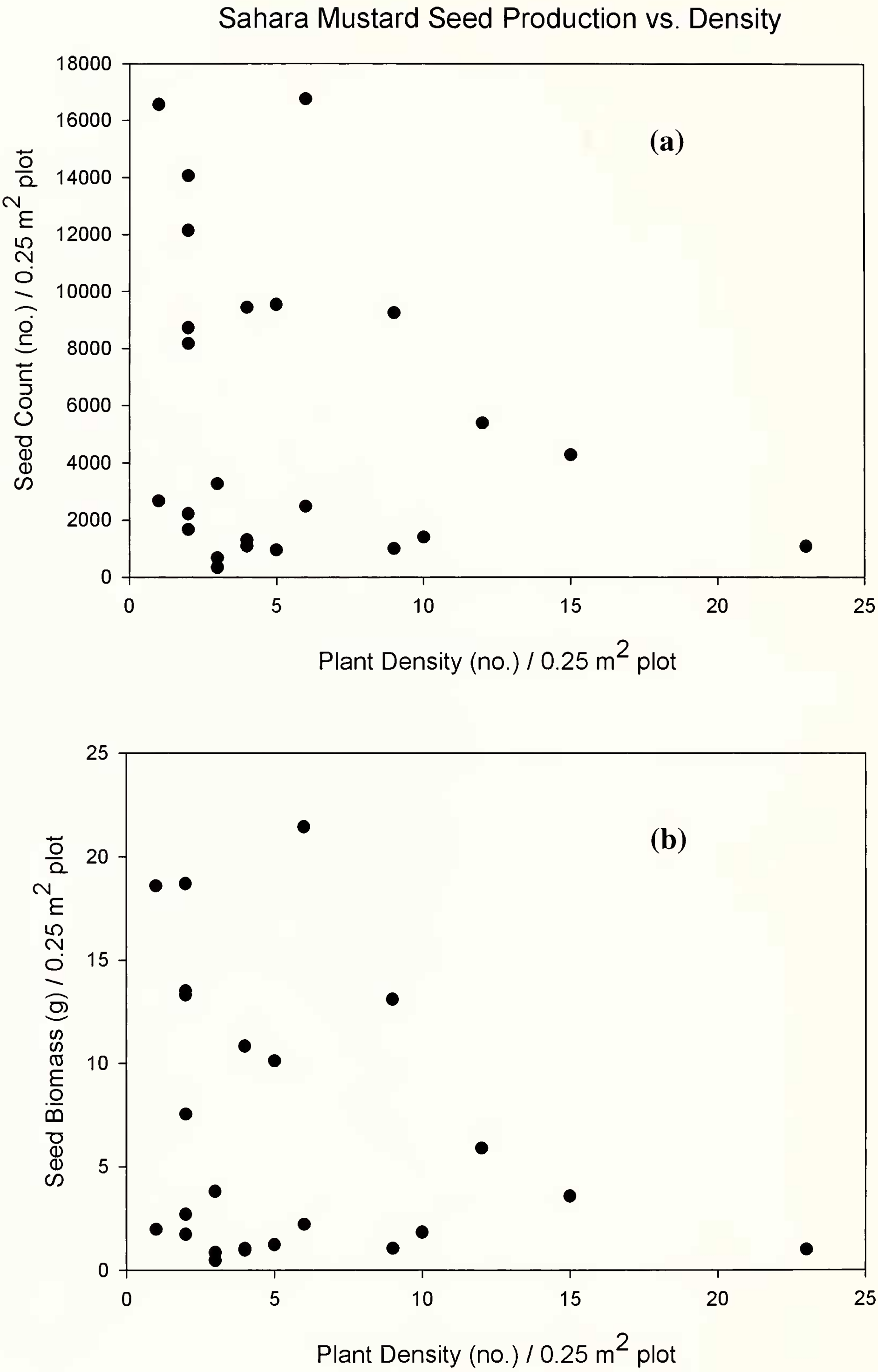


FIG. 3. **(a)** Scatter plot of seed count values related to plant density within a 0.25 m^2 plot. **(b)** Scatter plot of seed biomass values related to plant density within a 0.25 m^2 plot.

TABLE 2. PRECIPITATION AND DEPARTURE FROM NORMAL PRECIPITATION (CM) AT THREE WEATHER STATIONS NEAR THE NEEDLES, COACHELLA VALLEY, AND MOHAWK DUNES STUDY SITES (U.S. DEPT. OF COMMERCE 2003, 2004, 2005). * At time of preparation, only January–August 2005 precipitation data was available online.

Weather station	2003		2004		2005*	
	Precipitation (cm)	Departure (cm)	Precipitation (cm)	Departure (cm)	Precipitation (cm)	Departure (cm)
Needles AP	11.58	−1.40	16.08	3.10	12.95	4.29
Palm Springs	12.42	missing	19.86	missing	18.54	8.81
Yuma Proving Ground	9.14	−0.51	18.44	8.79	13.41	7.39

limiting resources and increased competition. Mean plant size and rates of emergence have been found to be negatively correlated with initial seed density in annual plant communities (Lortie and Turkington 2002). Species that have been recorded as producing fewer seeds at increased densities in the Mojave Desert include *Bromus madritensis* L. subsp. *rubens* (L.) Husnot (Harper 1961; DeFalco et al. 2003), *Vulpia octoflora* (Walter) Rydb., and *Descurainia pinnata* (Walter) Britton (DeFalco et. al. 2003), *Conyza canadensis* (L.) Cronq. (Palmblad 1968), *Pectocarya recurvata* I. M. Johnston, and *Plantago patagonica* Jacq. (Pantastico-Caldas and Venable 1993). Although not significant, the four plots in our study with the highest Sahara mustard densities had lower seed production than many plots with lower Sahara mustard densities.

The preliminary results mentioned in the Methods section indicate that microhabitat (beneath shrub canopy and interspaces between shrubs) and habitat (roadside and off-road) did not significantly affect seed production, but we believe this lack of significance to result from differences in soils at the three study sites. The Mohawk Dunes site has sandy soils which Sahara mustard prefers (Minnich and Sanders 2000), and can often dominate irregardless of other factors such as localized conditions created by shrubs and roads (Brooks accepted, M. Brooks personal observations). The soils at Needles and Coachella Valley are loamy and rocky, which Sahara mustard does generally not prefer, and where shrubs and roads can have a much stronger effect on dominance of this species (Brooks accepted). Variation in microhabitat and habitat effects among the three sites was one of the reasons for lack of statistical significance of these variables. Additional sites, replicates, and stratification of soils are needed to strengthen these ideas about Sahara mustard's habitat and microhabitat preferences.

MANAGEMENT IMPLICATIONS

Seed production should be considered when implementing control efforts and when creating effective follow-up strategies for any annual plant species, including Sahara mustard. The law of constant final yield and the results of this study suggests that plots that are only thinned during control efforts for Sahara mustard, leaving some individuals alive (e.g., hand-pulling or spraying a site once and not returning to look for survivors), may not reduce seed production and could inadvertently produce more standing biomass and have higher seed production than plots that are left untreated. The net result may be a more plentiful seed bank than would have existed if the smaller, less productive plants were left in place. Although this hypothesis remains to be tested, it suggests the importance of destroying all plants in a target area when control efforts are employed. This may require resurveys and follow-up treatments during the remainder of the growing season to locate and destroy plants that were missed the first time and to remove plants that have emerged since the initial treatments. Second and even third cohorts of Sahara mustard have been observed within the same growing season in the Mojave Desert (M. Brooks and M. Trader personal observations). Managers should be aware that this plant can produce several germination cohorts per year and that additional treatments may be required to remove all cohorts, as well as those which survived previous control treatments. It is therefore advisable to focus control efforts on repeated treatment and monitoring of smaller areas, than single treatments of larger areas.

As stated in the introduction, Sahara mustard poses threats to native desert vegetation. Currently, little information about this plant exists in the literature and additional research is necessary to create effective management plans. Information related to seed banks is specifically needed to evaluate Sahara mustard seed bank dynamics, seed longevity and persistence in soil, and the effects of plant density, microhabitats, and roads on seed production.

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